

# FIELDIANA • GEOLOGY

Published by

FIELD MUSEUM OF NATURAL HISTORY

Volume 16

MARCH 17, 1966

No. 1

## A New Shark of the Family Edestidae, *Ornithoprion hertwigi*

From the Pennsylvanian  
Mecca and Logan Quarry Shales of Indiana<sup>1</sup>

RAINER ZANGERL

CHIEF CURATOR, DEPARTMENT OF GEOLOGY

In the large amount of shark material that was recovered from the Mecca and Logan Quarry shales of west-central Indiana (Zangerl and Richardson, 1963), there is a very small, highly distinctive species of an apparently rare edestid shark. Among hundreds of shark remains, many of them partially articulated, the species to be described in the following is represented by only seven specimens from the Mecca quarry, by one from the Logan quarry and by one discovered by Mr. Vernon Lake, of Chicago, in the stripmine area, Peabody Coal Co., south of Wilmington, Illinois.

The specimens consist of intact or somewhat mutilated skulls and in three of them, postcranial skeletons reaching to the shoulder girdles. This type of occurrence is highly characteristic of the sharks of these localities in Indiana, and its ecological significance has been discussed elsewhere (Zangerl and Richardson, 1963).

### *Technical notes*

The study of these specimens, embedded as they are in a dense, carbonaceous shale, requires unusual techniques. It is absolutely out of the question to attempt removal of the shale from the fossil by mechanical means because the surface detail, of great importance to broad morphological questions, is measurable in microns, and hence beyond the capabilities of even the most skillful technician. The shale is extremely dense and resistant to chemical destruction, while

<sup>1</sup> While this paper was in press, Chicago Natural History Museum adopted the name Field Museum of Natural History. In this paper the catalog designations remain CNHM.

Library of Congress Catalog Card Number: 66-17461

No. 1004

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the fossils are soft and exceedingly brittle—delicate structures, such as minute placoid scales, may shatter if struck by a human hair used as a probe.

Some of the specimens were discovered by slight bulges on the bedding planes of thin slabs of shale and subsequent X-ray radiography. The specimens themselves have thus not been seen except as shadow pictures on film. Others were found while splitting the shale; in these the specimens are invariably broken along the bedding planes and are thus seen partly on the plate, partly on the counterplate. Specimens in this condition are very difficult to study and reveal little useful information on direct inspection.

For these reasons, radiographic techniques in conjunction with thin sections are the only feasible methods presently available for the study of this material. As will be seen, the techniques employed are on the whole highly satisfactory, but there remain some aspects of the organization of the animals that could not be solved.

The radiographic methods used in this study are as follows: stereoscopic roentgenograms were made of all but one of the specimens, with plates and counterplates properly superimposed and taped together where necessary for the purpose of picture taking. Since all specimens are reduced to essentially two dimensional state in the shale, the stereograms were made to grossly exaggerate the vertical depth perception across the shale slabs upon stereoscopic examination. This can be done simply by increasing the horizontal target displacement to about four inches at a target distance of two feet. Further exaggeration is possible, but tends to increase the difficulties of visualization. Fine-grained Kodak Industrial Film, Type B was used.

Because of the small size of the specimens even this procedure was not satisfactory. Both pictures of each stereo pair were next printed on film with the LogEtronic Contact Printer<sup>1</sup> which is essentially an electronic dodging device. The resulting film positives were next enlarged, again on film, in standard photographic fashion. This produced enlarged stereo negatives that could be viewed on a light-table. For reasons of convenience rather than necessity, I printed these enlarged negatives on paper, using the LogEtronic printer.

Films and paper prints were viewed with a standard stereoscope designed for the viewing of aerial photographs.

In order to produce the drawings (fig. 5) a highly translucent sheet of plastic with a drawing surface on one side (Dinoline Cartographic

<sup>1</sup> LogEtronics, Inc., 500 East Monroe Avenue, Alexandria, Virginia.

Sheeting<sup>1</sup>) was placed over one of the pictures of a stereo pair (which did not impair vision). Drawings could thus be made while viewing the three dimensional image, and there was no difficulty in determining which shadows belonged to what part of the specimen. The technique is perfectly reliable, and successful to the extent that the structural elements of the specimens have sharp outlines. Because of the nature of the preservation of this material (see below) this is not always the case.

The single specimen from Logan Quarry showed little promise, on X-ray pictures, of adding notably to what could be made out in all the rest. Yet, inspection of plate and counterplate revealed the presence of dermal denticles, teeth, and other interesting structures besides calcified cartilage. It was thus decided to use this specimen for a series of thin sections. Plate and counterplate were rejoined with an epoxy resin (Araldite 6005 with hardener No. 951<sup>2</sup>) and cut according to a predetermined pattern into pieces that were subsequently ground into thin sections. The position of all sections with regard to the specimen as a whole was marked on the slides.

In order to understand the limitations of the radiographic method used, it is necessary to recall some of the conditions of preservation of the material from the Mecca and Logan quarries, specifically as it applies to the material under discussion. Much of this has been discussed in an earlier account (Zangerl and Richardson, 1963). It may be briefly repeated here that all of the vertebrate specimens in this fauna show unmistakable signs of predation. In the present specimens, the body in back of the pectoral girdle was amputated, and the skull was mutilated in some cases. What was left of the carcasses settled into the bottom mud and was preserved almost exactly in the overall condition in which it arrived there. Bacterial decomposition, at first aerobic but very soon anaerobic, degraded the soft tissues including the uncalcified cores of the cartilage elements. Under a slight load of probably a few millimeters of sediment the skeleton settled essentially into a plane. The process was rapid enough to prevent mud from entering any of the cavities, for example, the brain cavity. Compaction or compression of the skeleton under a heavy load of sediment was not a factor in reducing the three-dimensional skeleton to virtually two dimensions. The skeletons of these

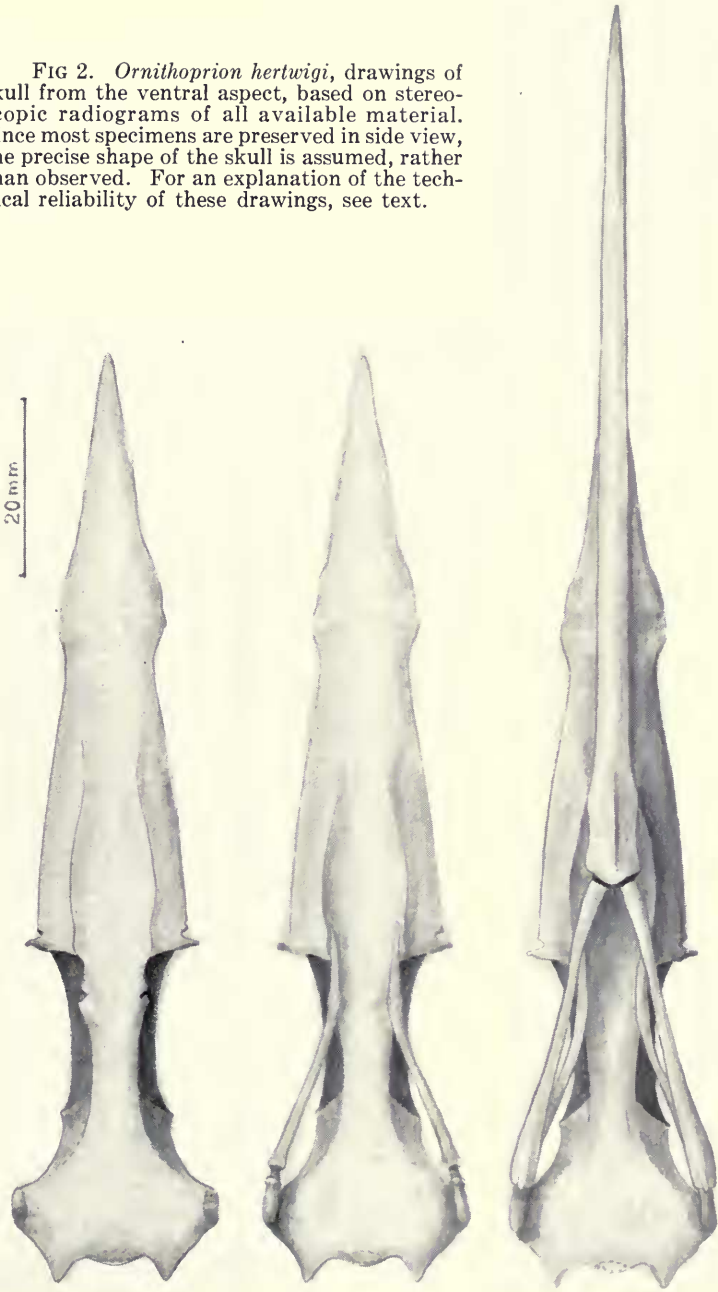
<sup>1</sup> Di-Noc Company, Cleveland, Ohio.

<sup>2</sup> Ciba Products Corporation, Fairlawn, New Jersey.



FIG. 1. *Ornithoprion hertwigi*, drawing of side view of skull (minus teeth), based on stereoscopic radiograms of all available material.

FIG 2. *Ornithoprion hertwigi*, drawings of skull from the ventral aspect, based on stereoscopic radiograms of all available material. Since most specimens are preserved in side view, the precise shape of the skull is assumed, rather than observed. For an explanation of the technical reliability of these drawings, see text.



sharks consist of calcified cartilage, i.e., each element is lined with tiny cubes of calcified tissue that form a pavement, but the individual cubes are not attached to each other except by uncalcified cartilage. In the process of burial and decomposition they remained in place and hence clearly define the boundaries of a given morphological element. In specimens that have been mouthed and thus more or less mutilated, these calcified cartilage prisms are no longer in their original locations and the boundaries of elements have been disturbed. Gas release during decomposition may also have disturbed these prisms in areas where much gas may have been vented, as for example, from the nasal capsules and the brain case. Both of these areas are poorly defined in the radiographs, even in specimens that show no evidence of mutilation in the region of the skull. Most of the specimens under discussion are preserved in side view, that is, they were buried in lateral position; in only one of them is the ventral portion of the braincase seen in nearly dorso-ventral view. For this reason the side view drawing of the skull (fig. 1) includes no assumptions save for the precise surface modeling of the chondrocranium. The ventral views (fig. 2), however, are true reconstructions in the sense that the width of the braincase, the curvature of the palatoquadrates, etc., had to be assumed. These assumptions were made on the basis of what appeared to me to have been the most likely original condition, and may, of course, be wrong.

Class Elasmobranchii

Family Edestidae

Genus **Ornithoprion**, new genus

CHARACTERIZATION

Very small edestid shark. Neurocranium, visceral skeleton and shoulder girdle consisting of calcified cartilage. Neurocranium with pointed rostrum, very large orbits and small postorbital extent; braincase apparently very small. Evidently no free hyomandibular. Palatoquadrates much reduced, do not meet tooth concentration on the neurocranium, anterior to palatoquadrates; palatoquadrates posteriorly attached by joint surfaces to lateral processes of neurocranium and near anterior ends to the ventro-lateral sides of the neurocranium by means of small "hook joints" (figs. 1, 2, 5b, 6). Meckel's cartilages short, high and thin, articulating with the palatoquadrates by means of double joints; anterior ends of Meckel's cartilages ending in vertical joint surfaces, articulating with an unpaired, extremely elongated mandibular rostrum that bears the teeth. Mandibular

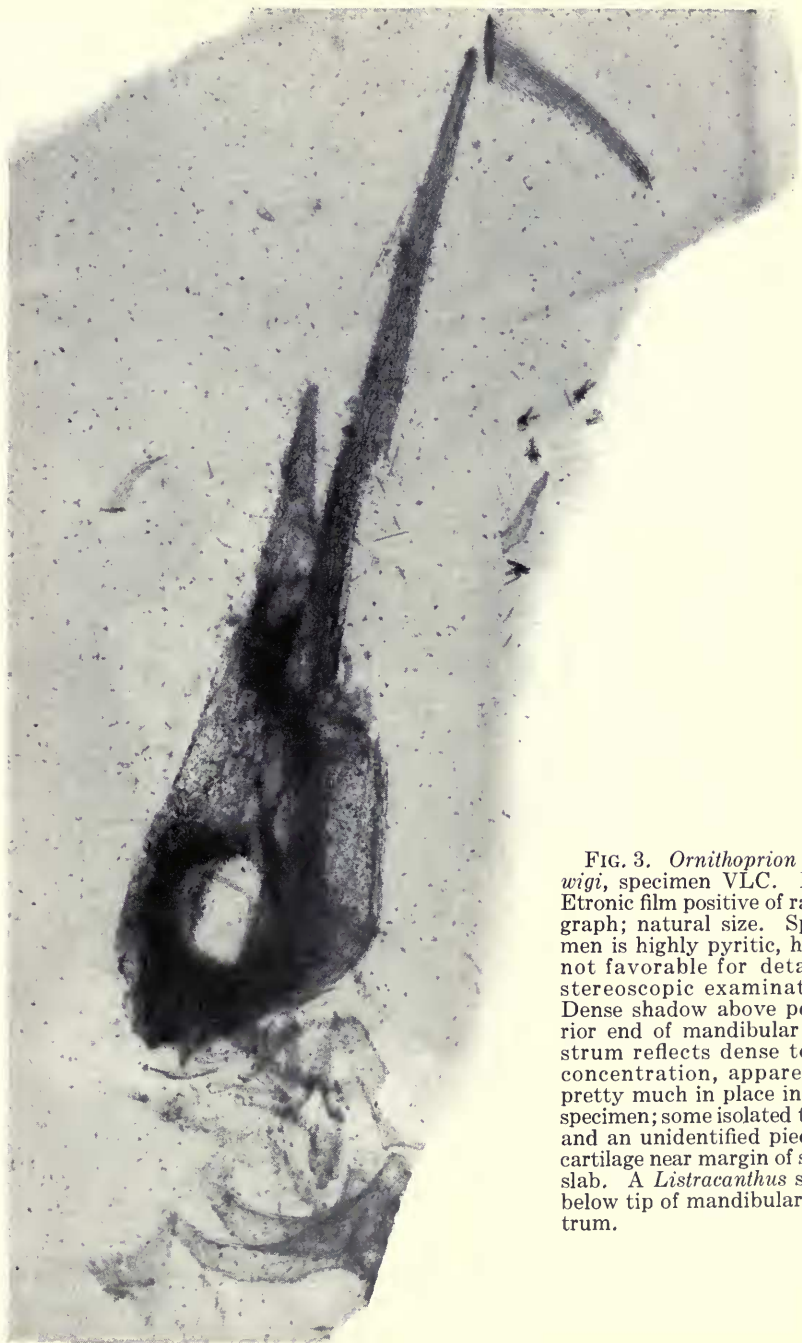


FIG. 3. *Ornithoprion hertwigi*, specimen VLC. Log-Electronic film positive of radiograph; natural size. Specimen is highly pyritic, hence not favorable for detailed stereoscopic examination. Dense shadow above posterior end of mandibular rostrum reflects dense tooth concentration, apparently pretty much in place in this specimen; some isolated teeth and an unidentified piece of cartilage near margin of shale slab. A *Listracanthus* spine below tip of mandibular rostrum.

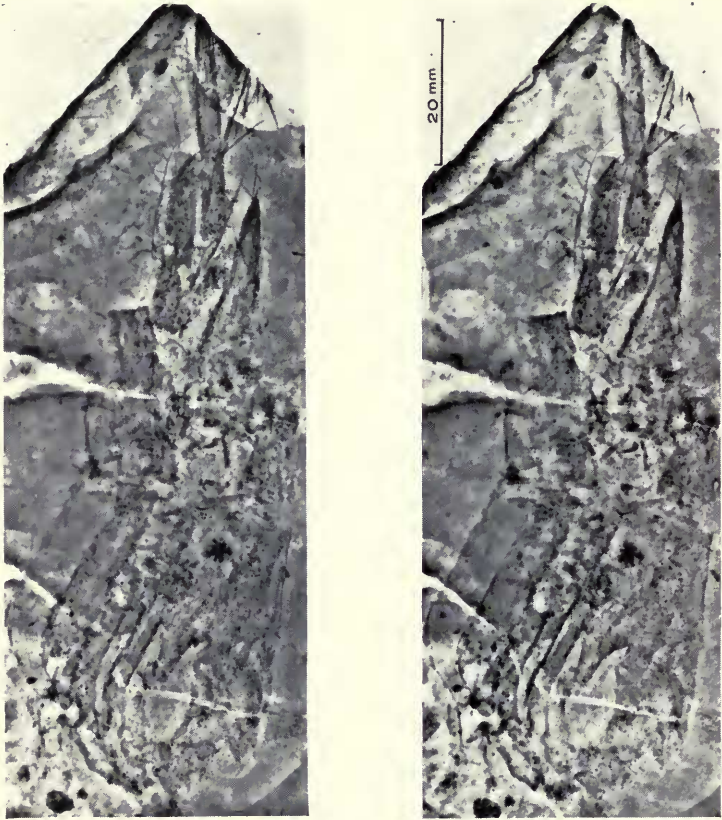
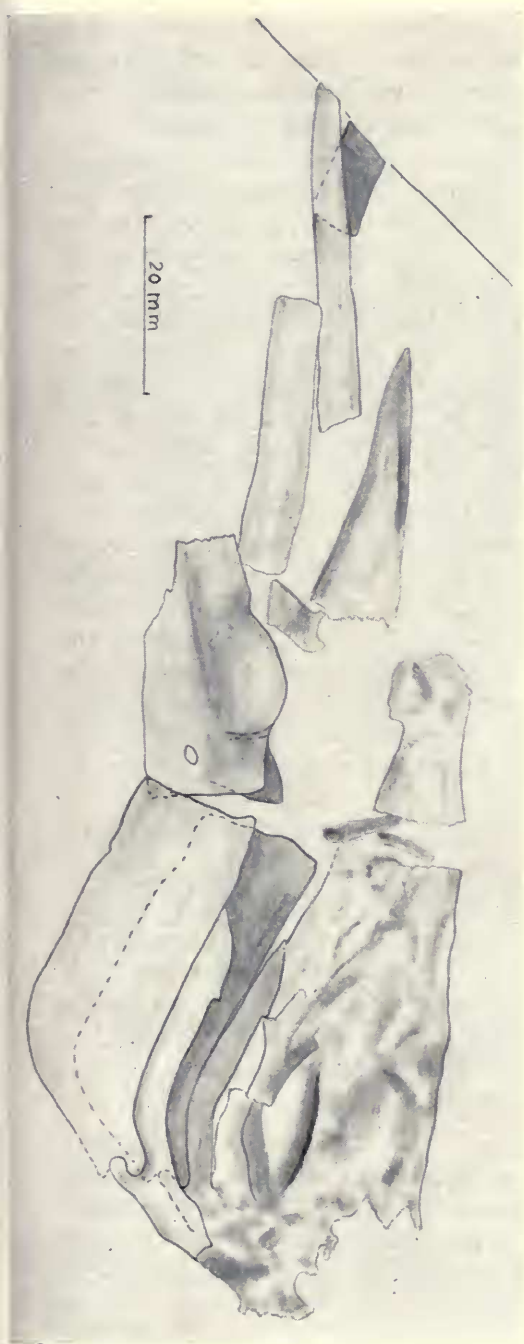


FIG. 4. *Ornithoprion hertwigi*, PF-2780. LogEtronic prints of stereoscopic pair of radiographs. Specimen in side position, but paired elements slightly offset.

rostrum posteriorly enlarged with ventral and lateral keel ridges and a dorsal semicircular (or semispherical) elevation bearing the enlarged symphyseal tooth row and the adjacent, lateral tooth pavement. Ceratohyals slightly larger than first pair of ceratobranchials. Probably five pairs of gill arches, probably arranged in order of decreasing size from first to last. Neural arches of the neck region of the vertebral column (pending confirmation of the elements in question as, indeed, neural arches) large, more or less leaf-shaped. Scapulo-cora-

FIG. 5. *Ornithoprion hertwigi*, a, PF-2780; b, PF-2923. Drawings made directly from stereoscopic pairs of radiographs. Compare a with fig. 4; b, with fig. 6. In b, base of neurocranium is seen in near perfect dorso-ventral view.





a



b

coids of standard selachian construction but scapular ends pointing forward, and with a grossly enlarged and elongated antero-median (sternal) element. Skeleton behind shoulder girdle unknown.

Dentition teeth of two kinds: enlarged upper and lower symphyseal teeth forming a row in typical edestid fashion, and very tiny bar-shaped teeth with low crowns forming a tooth pavement on either side of the symphyseal tooth rows. Detailed morphology of crown relief of the symphyseal teeth not discernible but probably similar to that of *Erikodus*. Symphyseal teeth consisting almost wholly of trabecular dentine; the peripheral layer of orthodentine being very thin. Small pavement teeth of similar histology. Mucous membrane denticles of simple conical shape with slightly curved crowns and bulbous bases, varying in size. Mucous membrane denticles consisting of ordinary orthodentine with narrow central pulp cavities and genuine bony bases. Dermal denticles ranging from simple denticles with genuine bony bases to composite scales consisting of two to seven or more fused denticles and a large mutual bony base. In the region of the snout and the mandibular rostrum active growth of the bony bases in antero-posterior direction as well as toward the cartilage skeleton. Fusion of the bases of adjacent scales producing longitudinal bony rods increasing in thickness toward the cartilage support beneath them, thus sheathing the tip of the snout and most of the mandibular rostrum with a coat of genuine bone.

**Ornithoprion hertwigi**,<sup>1</sup> sp. nov.

*Type*.—CNHM PF-2710, a nearly intact skull and posteranial skeleton back to the shoulder girdle. X-ray: MQ 55.

*Horizon and Locality*.—Mecca quarry, Level A3.4, Mecca Quarry shale, Liverpool cyclothem (Linton formation), approximately uppermost Westphalian, Pennsylvanian; Wabash Township, Parke County, Indiana (SW  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , Sec. 29, Twp. 15N. R. 8W.) about a mile from the town of Mecca (Zangerl and Richardson, 1963, figs. 7 and 10, Pls. 1 and 2).

*Referred specimens*

CNHM PF-2707, intact skull (lacking the tip of the snout, due to failure of early recognition of the find) and shoulder girdle. X-ray: MQ 200. Mecca quarry, level A3.4.

CNHM PF-2923, partially articulated skull. X-ray: MQ 193A. Mecca quarry, level A3.2.

<sup>1</sup> In honor of Oscar Hertwig.

- CNHM PF-2780, partly mutilated skull. X-ray: MQ 126. Mecca quarry, level B4.1.
- CNHM PF-2908, somewhat disarticulated skull. X-ray: MQ-193. Mecca quarry, level A3.2.
- CNHM PF-2824, badly bitten skull. MQ 190. Mecca quarry, level A3.3.
- CNHM PF-2903, a group of characteristic cartilage elements, and some teeth, on plate and counterplate. Mecca quarry level A4.2.
- CNHM PF-2656, mutilated, partial skull. X-ray: LQ 301. Logan quarry, level J. Logan Quarry shale, Lower Wiley cyclothem (Staunton formation), approximately uppermost Westphalian, Pennsylvanian, Reserve Township, Parke County, Indiana (NE  $\frac{1}{4}$ , SW  $\frac{1}{4}$ , Sect. 9, Twp. 16 N., R. 8W.) about  $1\frac{3}{4}$  miles east of West Union (Zangerl and Richardson, 1963, fig. 15, Pl. 3).

VLC, nearly intact skull and posterianal skeleton back to shoulder girdle. Highly pyritized. In the private collection of Mr. Vernon Lake of Chicago. From near Will County-Kankakee County line, between Wilmington and Essex, Illinois. Collected from slabs of black, carbonaceous shale on the spill heaps of strip mine. Exact stratigraphic horizon not known. Desmoinesian stage, probably Liverpool cyclothem, Pennsylvanian.

*Diagnosis.*—As for the genus.

## DESCRIPTION

### *Skull*

Of the nine specimens of this species now available for study, three present undamaged, articulated skulls in near-perfect lateral view (fig. 7, type PF-2707 and fig. 3, VLC). In specimen PF-2780 again in side position the posterior half of the skull is slightly disarticulated but all parts display their proper relations to each other. The anterior half, the snout and the unpaired mandibular rostrum, have been bitten into a number of pieces, but the relations between them are not in doubt. Apparently the mouthing did not sever the pieces entirely, but merely broke the internal skeleton. At the time of burial the broken parts were evidently still connected by the skin. This specimen, here illustrated by a pair of stereo radiographs (fig. 4), is far superior to the type for the study of anatomical detail. Another

specimen, PF-2923 (figs. 5b and 6), is of great anatomical interest because the ventral part of the braincase presents itself in near dorso-ventral view, revealing details of anatomy that are not visible in any of the other specimens. Specimens PF-2908 and PF-2824, though dissociated and chewed, exhibit some features that cannot be made out satisfactorily in the other specimens.

The predominant side position of burial of the skulls of this species suggests that the skull was relatively narrow and high, which in conjunction with the elongated pointed rostrum, the very prominent spike of the mandible, and the large size of the orbit imparts to the skull an overall similarity with that of a bird. The postorbital section of the skull is very short and the brain cavity must have been small. The absence of solid medial walls of the orbits strongly suggests that the orbits were separated from each other only by an inter-orbital septum, perhaps partly membranous. None of the specimens shows the structure of the inner ear, probably due to slight disarrangement of the calcified cartilage prisms in that area. In all specimens where the snout is preserved, there occurs at a morphologically comparable site a disruption of the pavement of calcified cartilage prisms. In all likelihood this represents the site of the nasal capsules. There are in all specimens two rather pronounced processes along the posterior margin of the braincase which might represent the imperfectly superimposed postotic processes. Slightly anterior to these there are more pronounced processes that end in joint surfaces, articulating with the palatoquadrates. In the modern *Heptanchus cinereus* (= *Heptanchias perlo*) and to a lesser extent in *Notorhynchus indicus* there is an articular facette beneath the postorbital process, a feature not observed in other groups of sharks by Holmgren (1941). The process in *Ornithoprion*, however, is too far behind the posterior rim of the orbit to be considered a postorbital process. The process in question, on the other hand, is properly located for a hyomandibular that might have become fused to the neurocranium (figs. 1, 10). The base of the neurocranium can be made out fairly well in PF-2923 (figs. 5b, 6). In the region of the orbits it is a narrow strip of cartilage that rapidly broadens out behind. The exact delimitation of the posterior portion could not be made out, but what can be seen suggests the arrangement illustrated in fig. 2. Close to the anterior end of the orbital region the base of the neurocranium broadens slightly to form small joint facettes along the margin, where the palatoquadrates are attached in front. Beyond this point the base of the neurocranium assumes the shape of a fairly broad trough, apparently somewhat curled up in specimen PF-2923. It is possible,

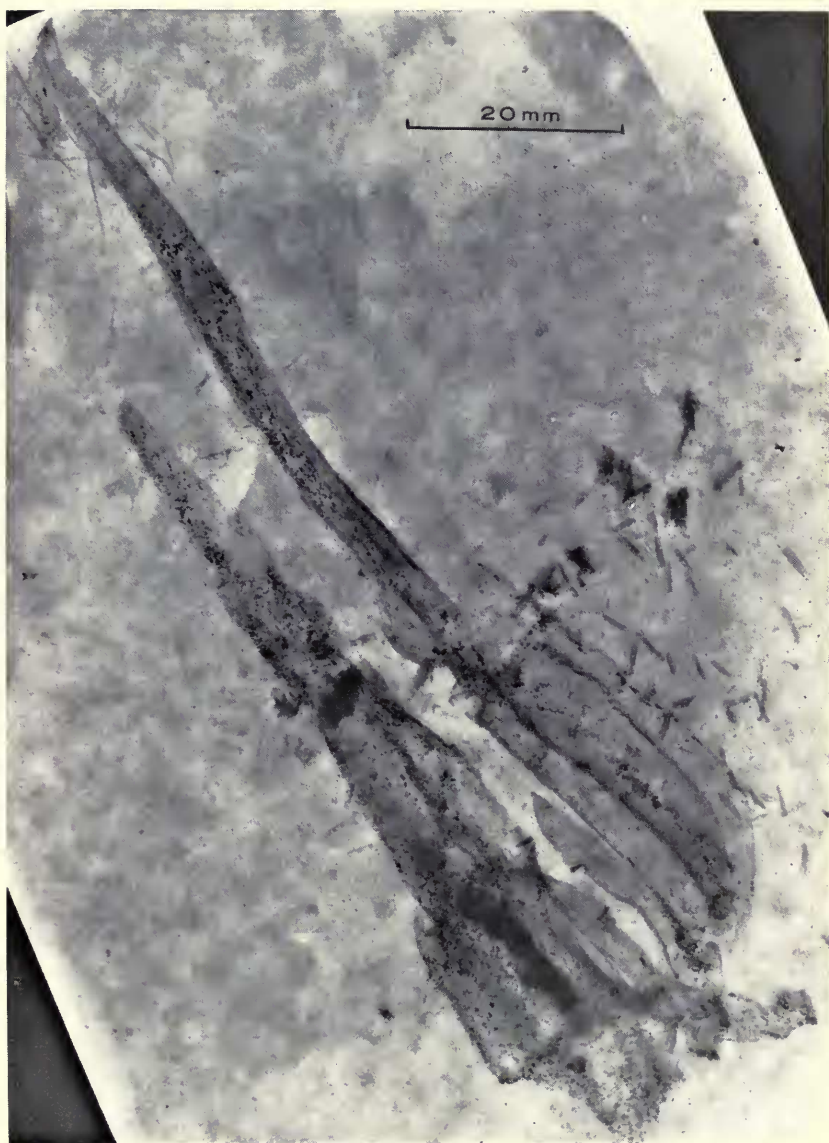


FIG. 6. *Ornithoprion hertwigi*, PF-2923. LogEtronic print of radiograph. (Compare with fig. 5b.)



FIG. 7. *Ornithoprion hertwigi*, type specimen PF-2710. LogEtronic print of a radiograph. Note dense accumulation of teeth above posterior end of mandibular rostrum. The specimen lies on the shale slab covered only by a thin film of shale; anterior end of mandibular rostrum was lost when shale was split and is visible as negative on the shale surface.



FIG. 8. *Ornithoprion hertwigi*, PF-2707. LogEtronic print of a radiograph. Ovoid shadow above posterior portion of skull is a coprolite that lies in a different bedding plane. Symphyseal and pavement teeth are fairly well visible.

however, that the trough as depicted in fig. 2 may be too wide. Within the anterior portion of the trough there is regularly a dense accumulation of teeth in all undisturbed specimens (figs. 3, 7, 8). These accumulations are well forward of the anterior ends of the palatoquadrates, and there would seem to be no doubt that the upper teeth of this animal were not attached to "jaws," (that is, to a visceral arch, the palatoquadrates) but were attached to the neurocranium proper. Although such a highly unorthodox condition has not been described before, it seems probable that *Ornithoprion* is not the only edestid shark in which this condition is realized. Nielsen, 1952, described a skull fragment of a moderately large edestid from Greenland, *Sarcoprion edax*. The specimen consisted of a portion of the front end of a skull containing both upper and lower symphyseal dentitions and lateral tooth pavements. The fragment was broken transversely into a number of smaller sections, thus revealing the internal structure of the forward part of the skull. The upper symphyseal teeth rested in a broad trough beneath the snout region. Nielsen searched in vain for an indication of a boundary line between the palatoquadrates and the neurocranium (on the cross breaks) and concluded, reasonably, that the palatoquadrates must be fused to the neurocranium. This may, of course, still be the case in *Sarcoprion*, but in view of the situation in *Ornithoprion*, it is no longer the only reasonable interpretation.

The palatoquadrates of *Ornithoprion* are narrow thin bands of cartilage with a very characteristic shape (figs. 1, 6, 9). They are strongly curved in side view and possess three joint surfaces, one of which is double, that is, it consists of a joint cavity as well as a joint head (figs. 1, 4, 5). The palatoquadrate is attached to the neurocranium in two places; at its posterior (or dorsal) end it is attached to a lateral process in the otic area of the skull which might represent a fused hyomandibular. Farther forward it connects by means of a "hook joint" with the ventral wall of the neurocranium (figs. 1, 6). Only a short distance in front of the "hook joint" the palatoquadrate ends rather abruptly in a point. The curvature of this element as depicted in ventral view (fig. 2) is hypothetical.

The lower jaw is a most unusual structure. It consists of two short, very high and very narrow cartilages that articulate posteriorly with the palatoquadrates by means of double joints, and end anteriorly in vertical joint surfaces that articulate with an unpaired, very much elongated cartilage, the mandibular rostrum (figs. 1, 2, 3, 6). This rostrum bears the teeth. To my knowledge, this curious



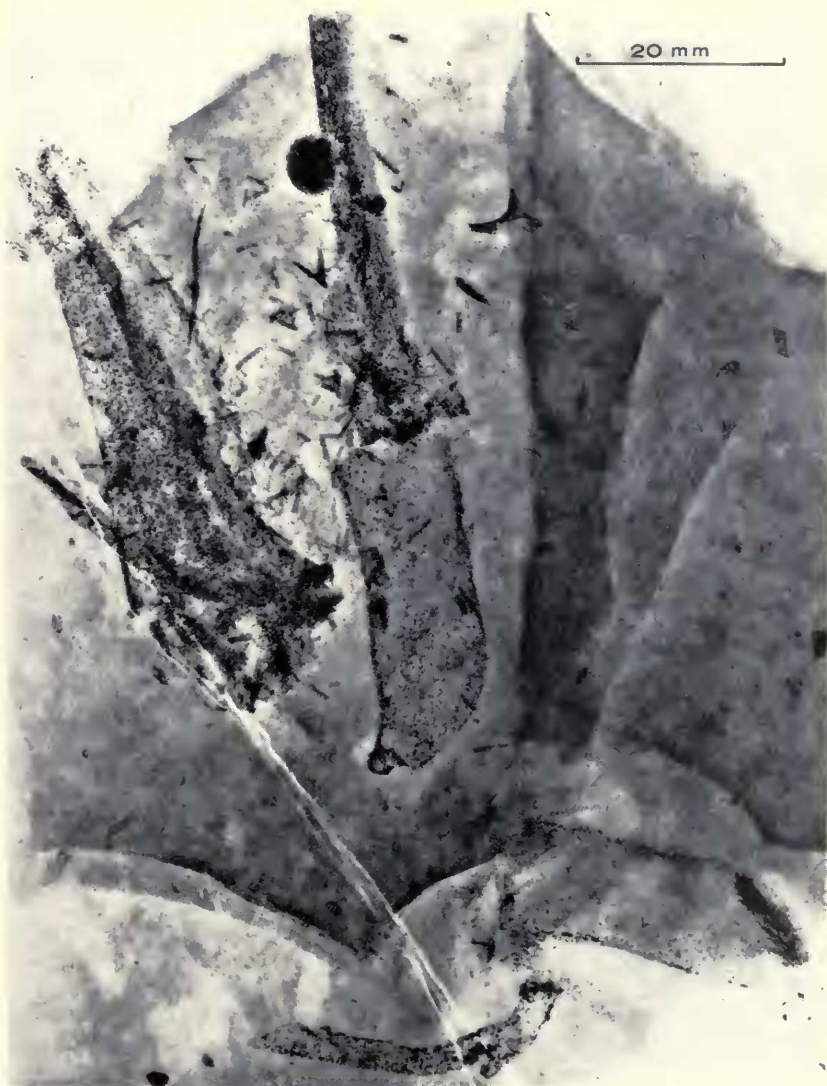


FIG. 9. *Ornithoprion hertwigi*, PF-2908. LogEtronic print of a radiograph. Neurocranium incomplete in back; palatoquadrate and paired portions of Meckel's cartilages disarticulated; one palatoquadrate near bottom of figure, the other lies diagonally across the neurocranium. Large black spot along mandibular rostrum is a *Petrodus* denticle and obliquely to the left of it there is a dorsal spine of an acanthodian—both are in different bedding planes. The teeth are widely scattered.

mandibular apparatus has no precedent among elasmobranchs, fossil or modern. Morphologically, the unpaired mandibular rostrum, however, is probably not a newly evolved cartilage element, but most likely represents the fused anterior ends of Meckel's cartilages. Fusion of Meckel's cartilages with rostrum-like elongation of the symphyseal region occurs in *Sarcoprion* (Nielson, 1952, fig. 7). The elongated symphyseal region bears the symphyseal tooth spiral. In *Ornithoprion*, aside from the presence of a joint immediately behind the point of presumed fusion, the row of symphyseal teeth occupies the same position as in *Sarcoprion* but the symphyseal portion has become greatly extended forward to form a long rod. The development of a joint immediately behind the symphyseal elongation is very probably a secondary feature, related to the mode of feeding of this animal.

The statement that the palatoquadrates and the posterior elements of Meckel's cartilages were very thin plates of cartilage (figs. 4, 6, 7, 8, 9) requires an explanation. It might be argued that the entire skull has been flattened into virtually a two-dimensional state as a result of anaerobic decomposition (see Hecht, 1933). How is it possible to state with reasonable certainty that a given cartilage element was thin prior to decomposition? The reasons are as follows: these elements have sharp outlines in all specimens and pretty much the same length-width proportions, and the pavement of calcified cartilage prisms is perfectly intact. Had these elements in life been oval or circular in cross-section, they would have had a much larger surface area than they do now; in the process of flattening to the present state the prism pavement would have become wrinkled or otherwise disrupted. Nowhere is there any evidence that an originally thick element was flattened by marginal expansion, as should be expected if physical compression had been the cause of flattening during decomposition.<sup>1</sup> The type of preservation of the Mecca material can best be described as a *vertical* projection of complicated surface relief onto a plane, as was observed in principle by Hecht (1933, p. 180) in an aquarium experiment. Hence, the interpretation as to the original thinness of the palatoquadrates and the posterior elements of Meckel's cartilages appears as a reasonable conclusion.

The mandibular rostrum was probably circular in cross-section in life, except for the posterior end which is much expanded, and shows

<sup>1</sup> There is absolutely no evidence that the flattening was the result of compaction or compression due to sediment load at a later date in the process of diagenesis; that is, *after* bacterial decomposition had ended.

a much more complicated cross-section. This part is provided with three longitudinal ridges, one ventral in the median plane, and two, probably smaller, lateral ones. On the dorsal side, just anterior to the joint facette, there is an elevation with the outline of a small section of a circle. This probably was a blunt median ridge in life. Specimen PF-2824 shows an intact series of symphyseal teeth "draped" over this area; this is also true in the type specimen PF-2710, but here the X-ray shadow picture is confused by the dense concentration of lateral pavement teeth that probably flanked the symphyseal row much as in *Sarcoprion* (Nielsen, 1952, fig. 15).

Elements of the visceral skeleton are illustrated in fig. 3 and fig. 12. Pieces of cartilage bars are seen in several specimens, but only in specimen VLC are such elements visible in adequate numbers to permit any idea as to the probable number of these elements and their relative sizes. In that specimen (fig. 12a), ten rod-shaped elements can be counted, and it is possible to match at least one pair of arches because they are clearly larger than the rest. These may have been the ceratohyal elements (Stensiö, 1963, fig. 84). The remainder of the visible rods make up an additional four pairs, probably ceratobranchials though it is not certain which specific rods belong to these pairs. In addition, there are a few smaller pieces that may represent a fifth pair of gill arches.

#### *Postcranial skeleton*

In the area where the vertebral column should be expected the type specimen PF-2710 shows a series of three rather large, vaguely leaf-shaped cartilages, followed by a poorly defined fourth and perhaps a fifth, above and behind the scapulocoracoids. Although none of the other sharks in the Mecca fauna shows cartilages of this shape and size along the vertebral column, I am inclined to believe that they represent highly modified neural arches. In none of the Mecca sharks is there even the faintest indication of vertebral centra, but neural arch pieces occur in many specimens and haemal arches are present in the region of the tail peduncle. It is possible that the unusual specializations of the skull are somehow reflected in the morphology of the vertebral column, but additional material is obviously necessary before such an analysis becomes meaningful.

Dorsal to the leaf-shaped elements there are other fainter shadows (fig. 11), with vague or no discernible outlines. Most likely these shadows represent remains of the skin (thus accumulations of shagreen denticles).

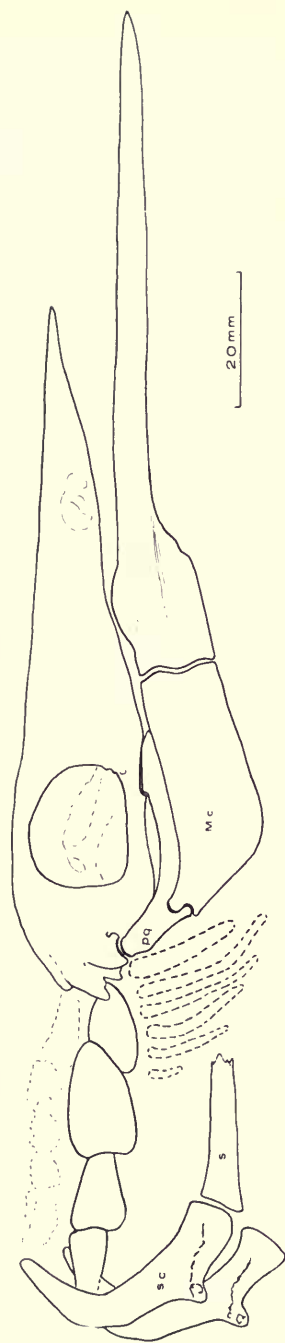


FIG. 10. *Ornithoprion hertwigi*, n. gen. and n. sp., reconstruction of skull and anterior part of thorax in side view, based on several specimens.

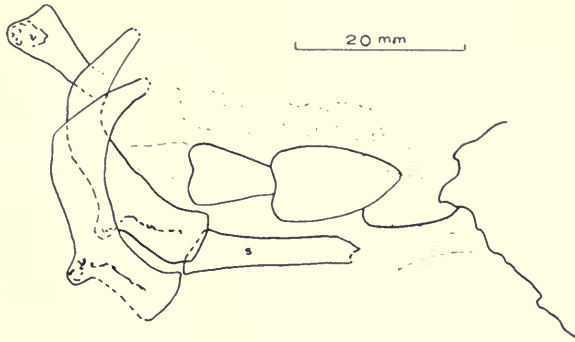


FIG. 11. *Ornithoprion hertwigi*, type specimen PF-2710, portion of postcranial skeleton; drawn from stereoscopic radiographs.

The shape of the scapulo-coracoids can be made out in several specimens (figs. 11, 12). Postero-laterally there is a prominent tubercle for the articulation of the pectoral fin base. The construction of these elements follows the standard selachian pattern except that the curvature of the scapular portion is anteriorly concave as seen in side view. That is, the dorsal end of the scapular part points forward, instead of backward, as seems to be the pattern in modern sharks. Furthermore, the coracoidal portion has a relatively greater antero-posterior extent than, for example, *Squalus sucklei* (CNHM 5249), or *Carcharinus velox* (CNHM 8170), of which X-radiographs are available for comparison. In front of the coracoidal portions of the shoulder girdle there is an elongated, rather large cartilage element that extends forward, probably beneath the gill basket (figs. 10, 11). Separate, median cartilage elements, though very small, have been reported by Haswell (1884), and later by Parker (1891) in *Notidanus indicus*. Parker showed that this element is the product of fusion of detached ventral ends of the girdle elements and calls it omosternum. According to Kälin (1931) all median, endoskeletal elements in the shoulder area are to be looked upon as sternal elements. Thus, he considers the structures in question in the sharks as most primitive sterna. In view of the origin of these elements, Kalin (1938) proposed the term zonosterna for them.

There is no proof, of course, that the large cartilage piece in front of the coracoidal portions of the girdle elements in *Ornithoprion* is homologous with the zonosterna of modern sharks, but the positional relationships certainly suggest it. There are other ventral cartilage elements in the region of the gill basket in selachians, such as the basihyal cartilage and the basibranchials (Stensiö, 1963, fig. 84).

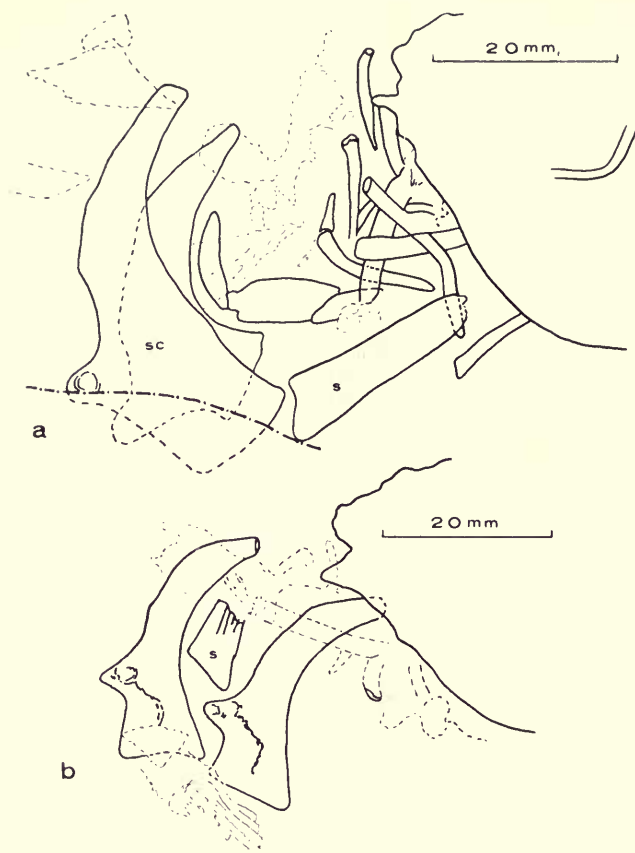


FIG. 12. *Ornithoprion hertwigi*, visceral arches and shoulder girdle. a, specimen VLC (see also fig. 3); b, PF-2707. Drawn from radiographs. Finely dashed outlines in "a" probably represent remains of the skin.

These, however, show lateral joint facets that articulate with the paired elements of the arches to which they belong. The cartilage rod in question in *Ornithoprion* shows no trace of such lateral articular facets; for this reason I regard it as unlikely that it might represent an element of this sort.

#### *Dentition teeth*

The teeth of the dentition of *Ornithoprion* consist of two kinds, enlarged symphyseal teeth and tiny rod-shaped pavement teeth. Both are visible on radiographs (figs. 6, 9), but because they are extremely small, I was not able to make out their surface appearance except in

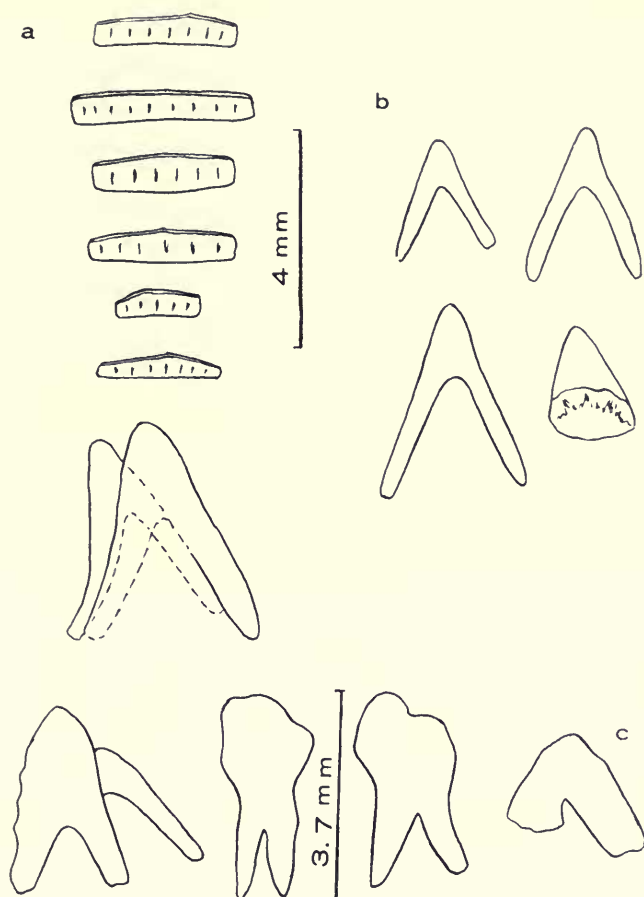


FIG. 13. *Ornithoprion hertwigi*, symphyseal and parasymphyseal pavement teeth, drawn from radiograph. a, PF-2923, bar-shaped teeth are parasymphyseal pavement teeth, V-shaped teeth probably belong to the upper symphyseal row; b, PF-2908, the conical element could not be identified definitely as a tooth or tooth fragment; c, specimen VLC (for description see text).

principle. The upper and lower symphyseal teeth appear to have notably different shapes. The V-shaped symphyseal teeth of fig. 13a, b, c, appear to belong to the upper dentition. The large tooth fragment in the thin section (fig. 14) probably represents the apical portion of one of the V-shaped teeth. The curious shadow outlines in fig. 13c, to either side of the scale line, probably represent lower symphyseal teeth (in anterior or posterior view). In specimen PF-2780 the lower symphyseal series is preserved intact (though barely visible in the

radiograph). Since the teeth were broken approximately along the sagittal plane when the shale was split, it was possible to remove the spongy trabecular dentine from the interior of the teeth on one side (counterplate) which provides an approximate idea of the shape of the crowns of these teeth, though not of the actual crown surface, because the outermost mantle of the teeth could not be removed (fig. 15b). Seven globular teeth compose this series. Their bases form a fairly thick platform, the structure of which cannot be made out. The anterior teeth are a little smaller than the posterior ones, and the base is thickest beneath the foremost tooth. It would seem reasonable to assume that the anterior teeth are the functional teeth, and the larger posterior ones, the replacement teeth.

The inner surface of the peripheral coat of what is assumed to have been orthodentine (see below), visible after the removal of the trabecular dentine, is nearly smooth except near the bases where there are some irregular wrinkles, as indicated in fig. 5b.



FIG. 14. *Ornithoprion hertwigi*, PF-2903, slide no. 4658. Section through large tooth fragment, probably representing crown of upper symphyseal tooth. Above it and to the right, various sections of parasymphyseal pavement teeth.



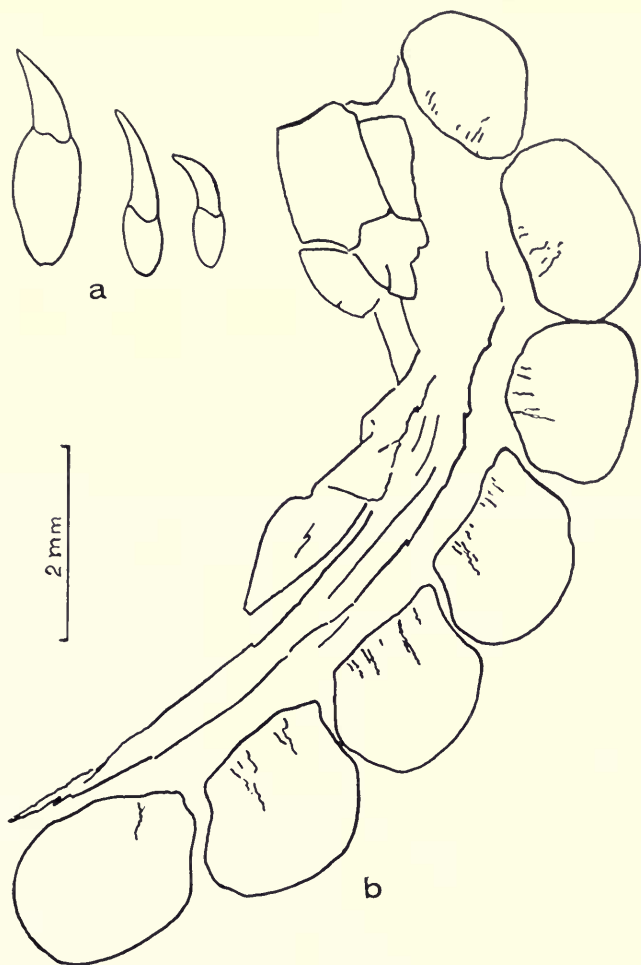


FIG. 15. *Ornithoprion hertwigi*, PF-2780. a, presumed mucous membrane teeth, drawn from specimen directly; b, lower symphyseal tooth row, drawn from a photograph; teeth near bottom of picture are replacement teeth.

A section through what I believe to be a lower symphyseal tooth is seen in fig. 16; I believe the section is close to sagittal. Part of the base, near the lower side of the picture, is broken off.

The rod-shaped pavement teeth are seen on radiographs, figs. 6 and 9, and outline tracings were made from some of them (fig. 13a). These teeth are of relatively simple morphology: a low crown with a slightly higher base. Along the sides of the base there are a number

of fairly deep pits (whether there are pits along one side and corresponding prongs on the other could not be determined). These pavement teeth are present in fairly large numbers.

The crown relief of both symphyseal and pavement teeth is probably more complicated than can be made out in the present material and with the techniques available. Suggestions to this effect are seen here and there in the broken specimen PF-2780, and in the thin sections, but none of this permits an adequate description.

#### *Mucous membrane denticles*

In addition to the dentition teeth there are large numbers of simple conical teeth with enlarged bulbous bases (fig. 15a) that are here

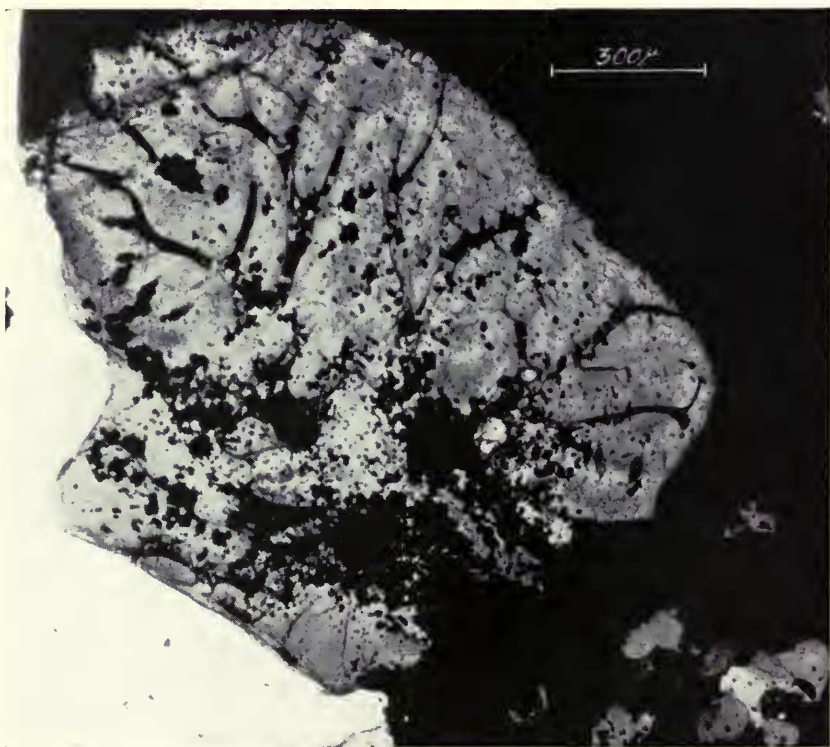


FIG. 16. *Ornithoprion hertwigi*, PF-2903, slide no. 4659. Section through large tooth fragment, believed to belong to the lower symphyseal tooth row. The lower left edge of the tooth corresponds to its base, which is broken off in lower center of picture.

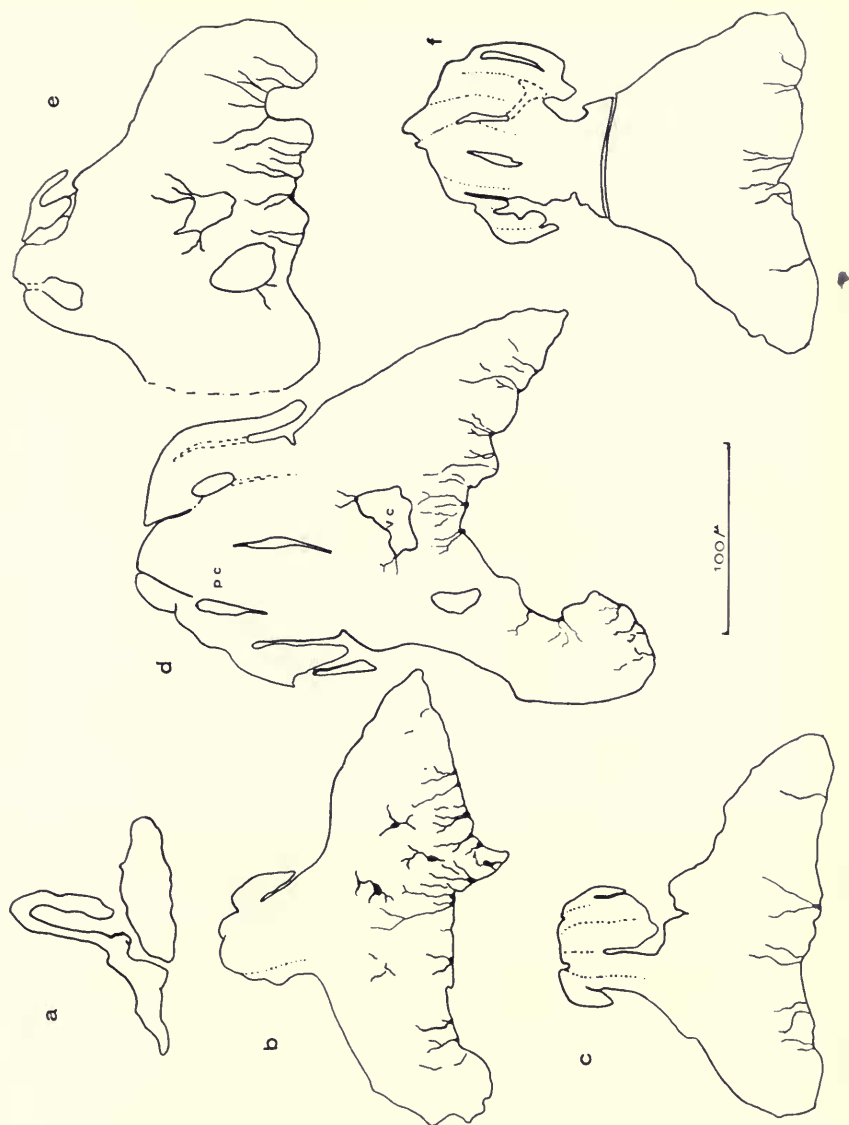


FIG. 17. *Ornithoprion hertwigi*, PF-2656, slides 4652 to 4656. Dermal denticle and compound scales. a, single denticle with large bony base and simple pulp cavity; b to f, compound scales with pulp cavities (pc) seen in the region of the crowns. The figures show the differences in the sizes of the crown regions, which is not necessarily due to greater complexity (compare d with f); scale e shows crown notably worn. vc (in d), vascular cavity.



FIG. 18. *Ornithoprion hertwigi*, PF-2903, slide no. 4652. Three dermal compound scales showing the crowns composed of several denticles, each with a pulp cavity and lateral openings to the outside of the scales. Beneath each crown there is a large bony base with canaliculi of bone cells extending into the bone from the base surface. (See also fig 23a.)

interpreted as mucous membrane denticles. This is admittedly an assumption that cannot be proven on the basis of present specimens. These denticles are generally located in the area of the mouth cavity, often in clusters. They vary in size from about 2 mm. in length to less than 1 mm. The thickness of the bulbous base also varies greatly.

#### *Dermal denticles*

These are highly interesting structures. The simplest form is a single denticle with a crown height of about  $50 \mu$  and a more or less extensive base. More often, however, the crown is a composite struc-

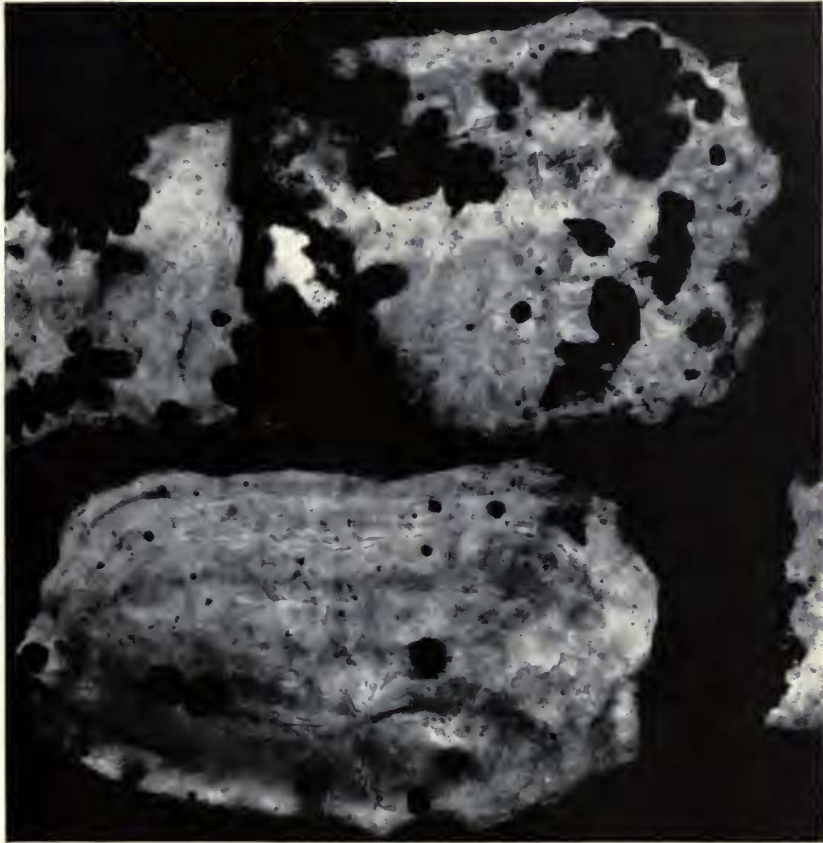


FIG. 19. *Ornithoprion hertwigi*, PF-2903, slide no. 4652. Thin-section through a number of calcified cartilage prisms from the region of the mandibular rostrum. Angular black areas are pyrite crystals.

ture consisting of two to seven or more denticles that have combined to form a highly distinctive crown with a mutual base (figs. 17 and 18). Because of their minute size, they are best seen in thin sections. Unfortunately, none of the slides shows the crown of any of these denticles in cross-section which would be helpful in ascertaining their precise morphology. The crown, furthermore, seems to have been subject to wear (fig. 17e). Single denticles as well as composite scales of this general type have been described from edestid sharks before (Nielsen, 1952, p. 34, pl. 9; Ørvig, 1951, p. 366 and Stensiö, 1961 and 1962) has rendered more or less diagrammatic illustrations of such structures. Ørvig and Stensiö have made them the starting

point for an elaborate theory intended to explain the morphological nature not only of the dermal denticles of modern selachians, but also of the teeth in vertebrates generally (see below).

#### THE MICROSCOPIC STRUCTURE OF THE HARD PARTS

*Calcified cartilages.*—Calcifications in the cartilage skeleton of *Ornithoprion* consist of a pavement of more or less cuboidal bodies that may be assumed to have occupied a position just underneath the surface of the cartilage elements, as is the case in many modern sharks. In thin-section they show concentric lines parallel to the surface (fig. 19), as well as around cartilage cells. Cells with what appears to be a complicated internal structure are clearly visible in fig. 20. Ørvig (1951) has described and illustrated similar lines in calcified cartilage, both modern and fossil, in what he called globular calcified cartilage.

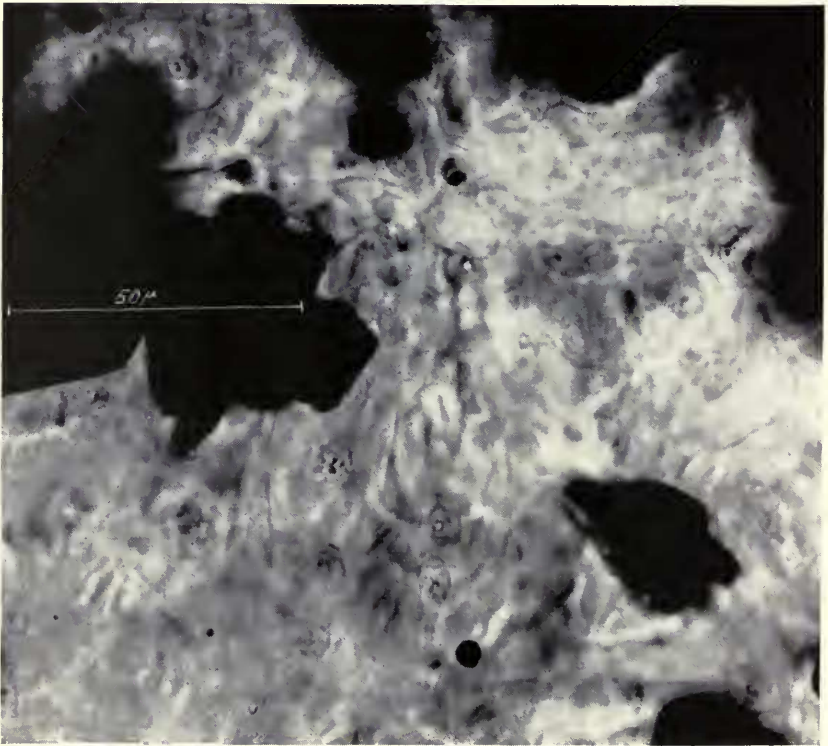


FIG. 20. *Ornithoprion hertwigi*, highly magnified portion of section shown in fig. 19. Note cartilage cells and more or less concentric lines around them.



FIG. 21. *Ornithoprion hertwigi*, PF-2903, slide no. 4657. Section through a fairly large, unidentified tooth showing the nature of the trabecular dentine.

*Dentition teeth.*—The symphyseal and the pavement teeth consist almost wholly of trabecular dentine. In specimen PF-2780, where nearly all teeth are broken and divided on plate and counterplate, there is one pavement tooth that shows the crown surface. This has the usual shiny appearance of shark teeth, but the ridges on the crown are altered into an amorphous brown substance. The outermost layer of virtually all of the broken teeth likewise shows this brown substance immediately above the trabecular dentine. Evidently the outermost layer, which probably constituted the orthodentine with its vitrodentine surface, has been destroyed in this material. The thin-sections bear this out. In none of the numerous tooth sections is there any sign of orthodentine left. Hence the vascular canals of the trabecular dentine seem, in many places, to open to the crown surface—a condition that can hardly be considered as primary (figs. 14 and 16). There appears to be no separate interstitial tissue between the circumvascular trabecular dentine and there are no clearly defined so-called dentinal osteons (fig. 21). The tooth bases consist of true bone with clearly defined bone cell spaces.

*Mucous membrane denticles.*—In contrast to the dentition teeth the conical mucous membrane denticles consist of a thick coat of orthodentine only (fig. 22). To judge from the surface appearance of the crowns, it may be assumed that a thin film of vitrodentine is present also, but this was not observed in thin-section. The pulp cavity is a single narrow canal that broadens near the base which consists of bone (fig. 22d).

*Dermal denticles.*—The crowns of the dermal denticles consist of what is assumed to be orthodentine; perhaps because of their tiny size dentinal tubules are not visible except occasionally near the pulp

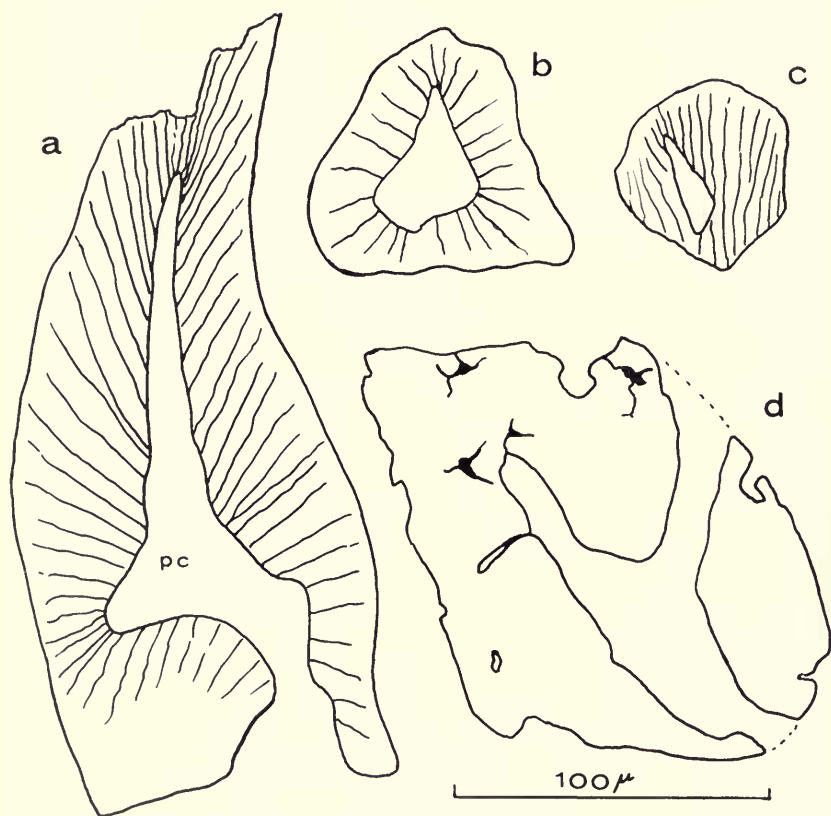


FIG. 22. *Ornithoprion hertwigi*, PF-2656, slide no. 4659, presumed mucous membrane teeth. a, in longitudinal section showing orthodentine enclosing a simple pulp cavity (pc); b, cross-section near the middle of the crown; c, oblique section near apex of denticle; d, cross-section near bottom of base showing bone with bone cell spaces.

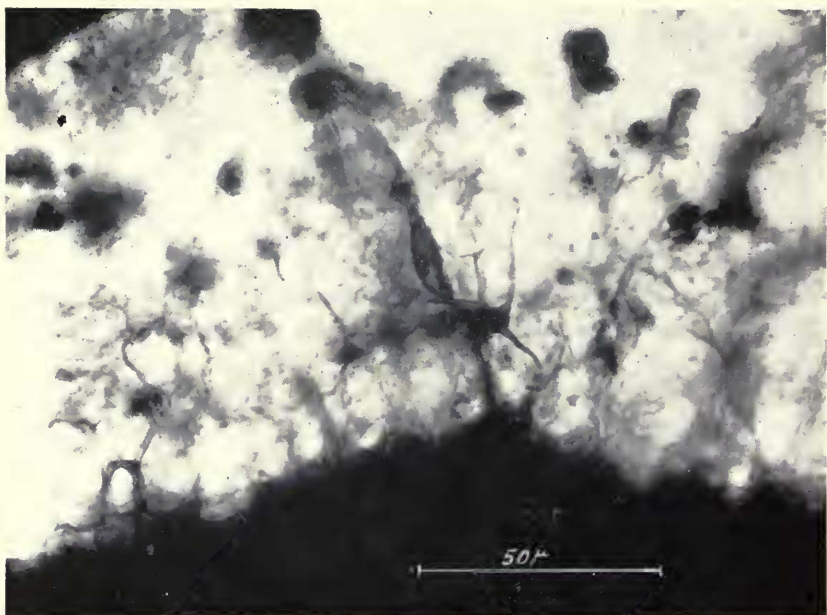


cavity. Each component denticle in a compound scale seems to have its own pulp cavity, but these are sometimes seen merging near the base of the corona. In a number of scales a lateral opening to the outside was observed (fig. 17c and f).

The bases of the single denticles as well as of the compound scales consist of bone. Bone cells (or their cell spaces filled with a brown organic precipitate) are seen within this tissue, but most abundantly along the basal margin from which they send canaliculi into the tissue (figs. 18 and 23a). It appears beyond doubt that the bases of these scales grew along the sides and along the inner margin (fig. 18). Moreover, the bases of adjacent scales fused to form antero-posterior rods (seen as very thin rods in the vicinity of the tip of the mandibular rostrum in the radiographs, figs. 4 and 6, and in the thin-section, fig. 23b), where part of a scale is attached to the rod. The rods clearly consist of bone which contains cell lacunae, but most of the cells are seen along the inner edges of the rods, which grew to notable thickness (fig. 24). Specimen PF-2780 shows that the tip of the snout and the mandibular rostrum are encased in a sheath of bone that surrounds the pavement of calcified cartilage. This relationship is also seen in thin-section (fig. 25).

#### PHYLOGENETIC RELATIONSHIPS OF ORNITHOPRION

The presumed phylogeny of the edestid sharks (Nielsen, 1952) is based largely on tooth morphology, inasmuch as very little is known about the cranial anatomy and virtually nothing is known about the postcranial skeleton. On the basis of what is now known of the teeth of *Ornithoprion*, there can be little doubt but that the genus resembles forms with relatively generalized, globular symphyseal teeth, such as in the Upper Permian genus *Erikodus*. Nielsen (1952) correctly suggested that forms with this type of symphyseal teeth should occur in the Pennsylvanian. In virtually every other respect, so far as comparison is possible, *Ornithoprion* is a very highly specialized animal. Concerning the suspension of the palatoquadrate, Nielsen (1952, p. 53) makes the following statement: "We now know that the jaw suspension in the typical Edestid *Sarcoprion*, also, (as well as in *Fadenia*, judging by well preserved skulls) is holostylic, and this must be regarded as another strong argument for including the Edestids as a whole in the large Bradyodont group." Eaton (1962) agrees with this interpretation. Unfortunately, the well preserved skulls mentioned have to my knowledge not yet been described, and the evidence, as presented for *Sarcoprion*, is subject to some doubt in



a



b

view of the findings in *Ornithoprion*. If the skull material of *Fadenia* does not show evidence of a separate palatoquadrate, as Nielsen implies, then it would seem more reasonable to assume that this element has been totally reduced in the Permian forms, in which case *Ornithoprion* would represent an intermediate stage in the phyletic process of reduction.

In view of the fact that the material from the Mecca and Logan quarries contains five different species of edestids, three of which will prove to belong to the more generalized sector of the family, it seems premature at this point to enter upon a broad discussion of the phyletic relations among the different known forms and the relationship of the family to other groups of elasmobranchs.

#### HERTWIG'S THEORY OF THE ORIGIN OF DERMAL BONES

In 1874 Hertwig proposed a theory of the origin of dermal bones in connection with the discussion of the significance of the dermal denticles in sharks. According to Hertwig, the dermal denticle of elasmobranchs is a simple morphological unit consisting of a tiny cone of dentine with a simple pulp cavity. At the base of the denticle, illustrated in section, Hertwig shows dense, interwoven connective tissue belonging to the dermis. This Hertwig regarded as an integral part of the denticle and suggested that it might ossify, thus forming a bony base. In a purely speculative fashion, Hertwig suggested that such bony bases might have fused laterally to produce bony plates beneath groups of denticles. By subsequent reduction of the denticles, dermal bones are presumed to have originated in the course of phylogeny.

This theory, although imaginative, met with serious difficulties in the decades that followed. For one thing, true bone could not be demonstrated in the bases of dermal denticles of sharks (although some authors have made the flat claim). Moreover, and much more important, the vast increase in our knowledge of early vertebrates has shown that the history of bone development is a more complicated matter than Hertwig had envisioned. For these reasons Hertwig's theory never enjoyed much credence among students of early vertebrates.

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FIG. 23. *Ornithoprion hertwigi*, PF-2903, a, slide no. 4653; b, slide no. 4659. a, basal bony part of a dermal compound scale, showing enclosed bone cell space with issuing canaliculi, and other canaliculi entering bone tissue from the basal edge. b, bony rods consisting of the fused bases of adjacent dermal scales; in top center the remains of a compound denticle.

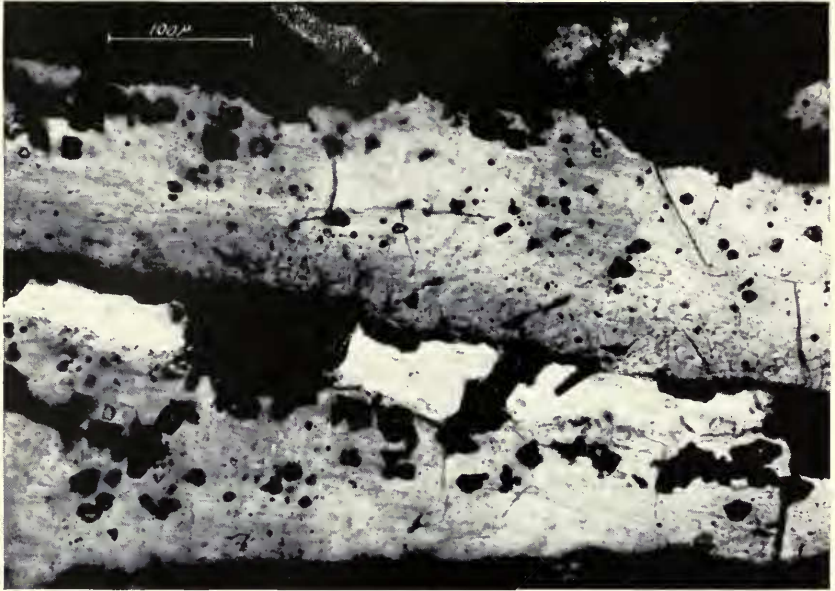


FIG. 24. *Ornithoprion hertwigi*, PR-2903, slide no. 4663. Bony rods, the product of fusion of the bases of dermal compound scales, showing concentration of bone cell spaces and canaliculi near lower edge of upper element, indicating that growth in thickness had not been terminated at the time of death of the animal. In the thin sections bone cell spaces and canaliculi are stained brown and are easily differentiated from pyrite crystals which are, of course, opaque.

It is thus of considerable interest to find an animal that illustrates Hertwig's theory most beautifully. The dermal denticles and compound scales of *Ornithoprion* do indeed have true bony bases, and there is good evidence to believe that these bases grew larger ontogenetically until they fused to form rods and finally plates.

The significance of these findings hardly lies in the area of the broad question of the phylogenetic origin of dermal bones in vertebrates; after all, *Ornithoprion* is a highly specialized member of a specialized group of late Paleozoic elasmobranchs. It is of notable interest, however, that Hertwig's speculations have indeed gained a basis in fact: dermal bone can, and did arise in the mode proposed by Hertwig in *Ornithoprion*. Whether it arose in this fashion in other groups of vertebrates, remains an open question.

#### THE STENSIÖ-ØRVIG LEPIDOMORIAL THEORY

Ørvig (1951) and Stensiö (1961 and 1962) have developed a theory that aims at explaining outright the morphological nature of scales of

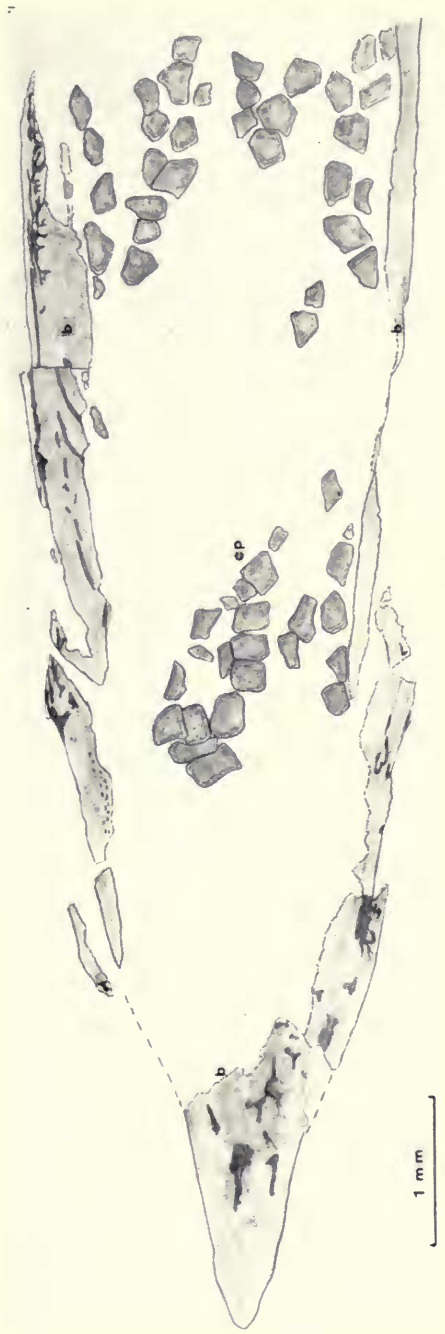


FIG. 25. *Ornithoprion hertwigi*, PF-2903, slide no. 4660. Section through prenasal rostrum showing a bony outer sheath (b) enclosing disarranged calcified cartilage prisms (cp).



FIG. 26. Whole mounts of lepidomorphous denticles and scales consisting of several lepidomorphous from a specimen tentatively identified as belonging to the genus *Agassizodus*, PF-2541. Note single lepidomorphous of different sizes, but identical morphology. Denticles as preserved are hollow and the walls are extremely thin as seen along the broken margin of the middle upper denticle.

fishes and even teeth in the vertebrates generally. Although the theory has been set forth in some detail, the underlying facts have as yet been presented only in rather diagrammatic form.

Compound dermal scales of an edestid shark from Greenland (probably *Sarcoprion*, see Nielsen, 1952, Pl. 9-1, and Stensio, 1961, fig. 1-X) were the starting point. Some of these scales are less com-

plex, consisting of fewer component elements (Stensiö, 1961, fig. 1-A to C). The components may be of different size, and there are single denticles (Stensiö, 1961, fig. 2, A, B, C). Unfortunately, the detailed morphology of these scales is illustrated only in diagrammatic form and it is therefore difficult to appraise the significance of the differences in the wall construction of the various scale components. On the grounds of these relationships the theory assumes that the simplest denticles constitute primordial units, called lepidomoria, which are said to consist of a coat of dentine (capped by enamel) surrounding a simple pulp cavity which is thought to have contained a single vascular loop, and a base consisting of bone. Because Devonian and Pennsylvanian elasmobranchs are known to have composite scales<sup>1</sup> that have, to quote Stensiö (1961, p. 237), "a bony basal plate of a laminate structure and are frequently of a rhombic shape," they are thought to resemble in both these respects "and in regard to their areal growth, . . . fundamentally the scales of, for example, ganoids, early porolepiforms, and osteolepids."

The occurrence of complicated scales in early elasmobranchs is thus considered as the original condition of the dermal armor in elasmobranchs. This together with the contention that individual lepidomoria are incapable of morphological differentiation or increase in size (also said to apply to "placoid" scales of post-paleozoic forms) led to the conclusion that even the simplest of dermal denticles (placoid scales) of modern sharks, as well as the teeth in general, are com-

<sup>1</sup> A prime reference for these early types of scales is provided by a paper by Gross (1938), on *Protacrodus vetustus* which Gross thought to be cladodontid shark. The scales of this animal are, however, of the same type as those of a large edestid from the Logan quarry (Zangerl and Richardson, 1963, pls. 24 and 25). In thin section they have shown to be very complex scales indeed, possessing not only the lamellar base mentioned by Stensiö (see citation above) but, in addition, a second basal tissue (different from the lamellar one) that is unmistakably bone, containing numerous well defined bone cell spaces. Although Gross could not make thin-sections from his material, it seems likely that *Protacrodus* is an edestid shark. In view of the variety of tooth structure and shape among the edestid sharks, I feel certain that the tooth shape of *Protacrodus* does not preclude its assignment to this family. The palatoquadrate of this form is perfectly well developed and of standard construction, which, no doubt, is the reason why Gross considered it a cladodontid shark. *Protacrodus* is a Wildungen specimen and hence of late Devonian age, thus very much older than any other recognized edestid. Since there is no reason to suppose that the edestids did not have their origin among the generalized cladodontids, the palatoquadrate of *Protacrodus* reflects the expected condition in an ancestral member of the Edestidae.

A survey of the dermal denticles in the cladodontid material from the Mecca and Logan quarries reveals that composite scales also occur in these forms, but they differ considerably from those of the edestids in shape and degree of intimacy of fusion of the component denticles (fusion seems to affect mainly their bases, not the crowns). Also, simple denticles occur along with a variety of complicated compound scales on the hide of the same individual, but in different places on the skin.

posites of lepidomoria that have become fused at the papillary stage of development. Ramifications of this theory concerning the scales of actinopterygians need not concern us in the present connection.

Any theory of this scope has, of course, notable theoretical interest. It would thus seem to be necessary that the factual background for the theory be carefully re-examined. Our contribution to the discussion is the discovery of dermal denticles in a specimen tentatively identified as belonging to *Agassizodus*, which are to be considered as lepidomoria of an even simpler type than those described by Stensiö. They consist of an extremely thin coat of dentine, surrounding an open pulp cavity, but they possess no bony bases. The smallest of these denticles observed measures  $175\mu$  in overall length and only about  $135\mu$  from the center of the open basal funnel to the tip. Individual denticles of this precise morphology, however, occur in different sizes, and there can be no reasonable doubt but that they are morphologically identical with the tiniest denticles, namely, single lepidomoria. Two or more of these elements, usually of different sizes, may combine to form a compound scale, whereby the lepidomorial nature of each component denticle remains clearly evident (fig. 26). The smallest denticle discovered in *Ornithoprion*, if we disregard the extensive bony base, measures little more than  $50\mu$  in height and has a total height of less than  $100\mu$  (fig. 17a). It has also a relatively large, undivided pulp cavity that extends as a vascular canal through the base and possesses a lateral foramen, precisely as do many of the dermal denticles of modern sharks, rays and skates, and has been postulated for single lepidomoria by Stensiö (1961). Tiny dermal denticles of the size range and morphology mentioned for the denticles of *Agassizodus* above also occur in modern elasmobranchs.<sup>1</sup>

The evidence presently available to me strongly indicates that, in contrast to the views expressed by Ørving and Stensiö, the compound scales of edestid sharks are not the primitive condition of the early elasmobranch dermal armor. Even in these forms, simple lepidomoria do occur (primarily on the ventral side of the body). Single lepidomoria, furthermore, vary in size. Their morphology appears to be identical in virtually every detail with that of the simplest types of dermal denticles in modern forms. Among the latter it is possible to follow step-by-step the differentiation of these denticles in terms of surface relief and size, but always retaining the same basic morpho-

<sup>1</sup> Excellent illustrations of a variety of different dermal and mucous-membrane denticles in modern forms, as well as microscopic sections at various stages of development, will be found in B. Peyer's forthcoming book on comparative odontology.



logical simplicity. In view of these facts, it seems an unnecessary complication to suggest that the dermal denticles of modern sharks are composites (synchronomoria) of lepidomoria, fused at the papillary stage. Instead, it seems that in the family Edestidae (and in other paleozoic groups of elasmobranchs) simple lepidomorial denticles combined in various degrees of complexity to form highly distinctive scales whose histological composition, in the most complicated cases, requires further study.

#### FUNCTIONAL CONSIDERATIONS OF THE SKULL OF ORNITHOPRION

The peculiar modifications of the skull of *Ornithoprion* recall those of the half beak *Hemirhamphus* (Teleostei), which feeds near the surface. The possibility that *Ornithoprion* might have fed near the surface also cannot be fully ruled out, but it would seem improbable in view of the fact that the teeth have a durophagous aspect. There are furthermore a number of peculiarities of construction that seem to be related to the function of the elongated mandibular rostrum. Both attachments of the palatoquadrate to the neurocranium and the double articulation of Meckel's cartilage with the palatoquadrate give the appearance of shock buttresses. Since the paired portion of Meckel's cartilage was probably only slightly movable against the palatoquadrates, and since the symphyseal teeth were anterior to them, we may assume that mastication took place between the unpaired mandibular element and the tooth-bearing part of the neurocranium. The great height of the paired portions of Meckel's cartilage is probably related to the restricted movability of the mandible, in the sense that this provided a permanently large mouth cavity. The bony sheaths around the tip of the snout and the mandibular rostrum are probably related to the functioning of the entire strange feeding mechanism.

Considering all of these features, we must assume that the mandibular rostrum performed some rather special function. Bottom feeders generally have subterminal mouth openings on the ventral side of the body (for example, rays and skates, and, for that matter, modern sharks generally, whether they are strictly bottom feeders or not). That the mandibular rostrum was well movable against the paired portions of Meckel's cartilages must be assumed in order to render the teeth functional. Almost certainly the adductor mandibularis and praeorbitalis muscles originated in front of the orbit, as in *Heterodontus* and *Stegostoma tigrinum* (Luther, 1938, p. 499, figs. 437 and 438), and were inserted on the enlarged posterior end of the mandibular rostrum.

It should be mentioned here that a morphologically analogous premandibular element is present in the Cretaceous teleosts *Saurodon* and *Saurocephalus* in which the unpaired pointed structure is a bone that articulates with the dentaries. The function of this element is not known, though the rather improbable suggestion has been made that it might have been used as a weapon of offense.

The functional significance of the grossly elongated mandibular rostrum in *Ornithoprion* remains a mystery, but it is possible that the animal used this device to stir up (and perhaps flip up) potential food animals from the bottom, and then proceeded to grasp them.

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